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ASPECTS OF THE ECOLOGY OF VASCULAR EPIPHYTES IN TWO COLOMBIAN CLOUD FORESTS. II. HABITAT PREFERENCES OF BROMELIACEAE IN THE SERRANIA DE MACUIRA

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In a previous paper (Sugden & Robins, 1979) it was shown that eight species of Bromeliaceae occurring in a cloud forest on the Serranía de Macuira, Colombia (12°N, 71°W) exhibit various preferences of habitat which may be related to levels of exposure to cloud, which in turn depend upon aspect and altitude. This cloud forest, which extends from 550 m to the summits of the Serranía (865 m), is remarkable in that it is surrounded by arid lowlands and depends entirely on the interception of moisture from clouds for at least 10 months of the year. Because of rugged topography and the virtually constant direction of the ENE trade winds, differences in exposure to wind result in a range of canopy height from 1-10 m (Figure 1). The cloud flux or throughput, and hence the levels of cloud interception by the vegetation is greatest when the wind is strongest. The duration of cloud cover increases with altitude; it is at least 12.5 h/night on 77% and 95% of nights respectively at 550 m and 700 m, and the highest peaks sometimes remain in cloud for up to 36 h. Because of the lack of rainfall, except during the rainy season of October-November, and the small altitudinal range of the cloud forest (which results in a narrow temperature range), the factors limiting the distribution of bromeliad species within the cloud forest are somewhat simplified.

In the present paper I wish to consider the habitat preferences of the eight bromeliad species in greater depth, since these plants can provide clues concerning the role of cloud cover in the maintenance of the vegetation, and, where possible, to relate these preferences to published data concerning physiology and morphology. Epiphytic Bromeliaceae have come to be regarded as good indicators of climatic conditions because of their complete independence of the substrate in terms of both water economy and mineral nutrition (Gilmartin, 1973). A considerable body of knowledge concerning the family has been assembled in recent years, covering aspects of the morphology, physiology, ecology and distribution of many species, including six of the eight species encountered in the Serranía de Macuira.

The Tillandsioideae, which are regarded (Smith & Downs, 1974) as the most advanced subfamily of the Bromeliaceae in terms of indumentum, are obligate or facultative epiphytes which take up water through absorptive peltate trichomes on the leaf surface (Mez, 1904; Benzing, 1970b, 1973; Benzing & Burt, 1970; Benzing & Renfrow, 1974, 1976; Benzing *et al.*, 1976, 1978). Benzing & Renfrow (1976) recognise two principal nutritional strategies in the Tillandsioideae, which are related to their habitat preferences and which manifest themselves in both gross morphological features and in the quantity and distribution of absorptive trichomes on the leaves. The first group, the mesic tank epiphytes, are characterised by their ability to impound water in the leaf axils, and by their sparse trichome cover and a general preference for humid habitats. Most of these species support small communities of freshwater organisms (Laessle, 1961, Gibson & Robins, 1976) whose waste products and decaying bodies provide an important source of nutrients for the plant. The second group. the atmospheric epiphytes, are unable to impound water between the leaf bases, having a very tightly-packed or re-

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duced rosette, and have a dense covering of peltate trichomes; these species exhibit a preference for xeric habitats. Water and nutrients are obtained directly from the rainfall or stemflow (Benzing & Renfrow, 1974) though in some cases water may be absorbed directly from atmospheric vapour (Virzo de Santo *et al.*, 1976). A few of the atmospheric bromeliads are myrmecophytes (Benzing, 1970a) and have been show to be capable of absorbing nutrients derived from the activities of ants inhabiting the bulbous base of the rosette. Many, probably the majority, of the atmospherics employ the CAM pathway of CO_2 fixation (Coutinho, 1965; McWilliams, 1970, Medina, 1973; Medina & Throughton, 1974), in common with many other xerophytes.

The bromeliads in the Serranía de Macuira range from the small atmospheric myrmecophyte *Tillandsia bulbosa* to the large mesic *Guzmania cylindrica*, which has leaves up to 1 m in length and a biomass of around 2.5 kg when mature. Some of the morphological and physiological attributes of the eight species are listed in Table 1, while their distribution within the cloud forest is shown in Table 2. The individuals were counted by eye, and separate assessments were made of the populations growing above and below 'half canopy height' -- the distance midway from the ground to the top of the canopy -- thus distinguishing the individuals growing on the boles and lower branches from those in the canopy. Vegetative specimens of each species are easily identified, provided that they are of adult or sub-adult size; the figures in Table 2 refer to all those individuals with longest leaf > ca. 10 cm. For a complete account of the methods used in scoring the epiphytes, see Sugden and Robins (1979). In the following paragraphs, in which each species is considered separately, the results obtained in this survey are compared with those of Pittendrigh (1948), who, in a semi-quantitative survey of the ecological distribution of bromeliads in Trinidad, recorded six of the eight species found in the Serranía de Macuira and ranked them according to their requirements of light, humidity and precipitation.

Tillandsia bulbosa Hooker.

Ninety-five percent of the individuals of *Tillandsia bulbosa* were observed in one plot, a leeward slope at 600 m; the remainder were observed in one of the gullies (Plot 14). Similar numbers of individuals occurred above and below half canopy height. Other observations indicated that it occurs very sporadically in the cloud forest, mainly at or near the transition zone with the surrounding dry vegetation. *Tillandsia bulbosa*, a lowland species, has more xeromorphic features than any of the other seven species. It has short, thick, curled leaves which are tightly packed at the base, and no tank. It has a high compensation point, low photosynthetic efficiency at low light intensities and 100% trichome cover on the adaxial leaf surface (Benzing & Renfrow, 1971a). Medina (1973) has shown that it has a high light requirement, growing mostly in deciduous forests, and that it has CAM metabolism. Pittendrigh (1948), however, suggests that *T. bulbosa* prefers heavy to moderate shade in Trinidad, although he admits to a paucity of data. Nevertheless, he proceeds to observe that it is certainly rarer than *Guzmania lingulata* in shaded habitats, occurs in well-lit cacao plantations from which *G. lingulata* is absent, and that it tolerates annual rainfall of 1250 to 3125 mm.

Guzmania monostachya (L.) Rusby ex Mez

Leeward slopes are favoured by *G. monostachya* and within this habitat the individuals are twice to four times as numerous on the boles and lower

TABLE 1. Some characteristics of the 8 species of Bromeliaceae encountered in the cloud forest. Sources: Benzing & Burt (1970), Benzing & Renfrow (1971 a, b), Medina (1971) & Throughton (1974), Pittendrigh (1948), Smith (1977).

	leaf length (cm)	leaf width (mm)	% trichome cover upper	% trichome cover lower	CAM	Compens-ation point (ft.-c.)	Altitudinal distribution (m)	Rainfall zones in Trinidad (mm)
Tillandsia bulbosa	7-22	2-7	100	30	+	84	0-1350	1250-3125
Guzmania monostachya	20-40	20	50	40	+/—	35	0-2000	1250-5000
Tillandsia anceps	15-40	7-12	25	30	—	40	0-1300	1750-5000
Guzmania lingulata	30-45	30-40	4	4	—	12	250-1100	1750-5000
Guzmania sanguinea	20-40	50-80	-	-	—	-	0-1050	3125-5000
Vriesia splendens	40-80	40-60	-	-	—	-	300-1300	2250-5000+
Vriesia heterandra	30-40	15-20	-	-	-	-	400-2300	absent
Guzmania cylindrica	80-120	50-80	-	-	-	-	600-1500	absent

branches as in the crowns. It is absent from windward slopes and sheltered ridges at higher altitudes, although it makes a significant contribution to the total bromeliad flora on the sheltered ridges samples at 600 m and 700 m (Plots 3 and 5). It is less frequent in gullies than on leeward slopes. *Guzmania monostachya* is generally the first bromeliad to be encountered at the transition of dry evergreen forest with cloud forest, though a few scattered clumps of *Tillandsia bulbosa* and *Vriesea heterandra* may also be present. These observations suggest a preference for well-lit, moderately dry sites, though partial shade is certainly tolerated; it is apparently intolerant of the conditions prevailing above ca. 750 m.

In Trinidad the most dense populations of *G. monostachya* occur in well-lit canopies where annual precipitation is from 1250 mm to 5000 mm (Pittendrigh, 1948), and in Venezuela where light intensity and humidity are high (Medina & Throughton, 1974). Benzing & Renfrow (1971.) collected it in full sun and partial shade in central America, while Laessle (1961) encountered it under more shaded conditions in very humid mist forest in Jamaica. It has a trichome cover of 40-50% on the leaves (Benzing & Renfrow, 1971a), which is consistent with a tolerance of relatively dry conditions, and it may be physiologically flexible in having the ability to employ either the CAM or the C_3 pathway of CO_2 fixation depending on environmental conditions (Medina & Throughton, 1974). Such flexibility may have contribut-

ed to the success of *G. monostachya* over a wide geographical range and from 0-1000 m.

Tillandsia anceps Lodd.

This small mesic tank species is most frequent on sheltered ridges at lower altitudes (600-650 m), and to a lesser extent, on leeward slopes at 600 m; it also occurs in significant quantities in the intermediate habitat sampled in Plot 8. It is very rare on windward slopes, gullies, and sheltered ridges above 650 m. Of the 160 individuals sampled altogether, only three were growing in the canopy. These observations place the habitat preferences of *T. anceps* between those of the larger tank species *Guzmania lingulata* and *G. monostachya*.

Pittendrigh (1948) includes *T. anceps* amonst the shade-tolerant bromeliads of Trinidad, where it occurs in rainfall zones of 1750 mm to 5000 mm. Its compensation point and photosynthetic efficiency at a given light intensity are similar to those of *G. monostachya* (Benzing & Renfrow, 1971a) though it does not have CAM metabolism (Medina, 1973). The percentage cover of trichomes is lower than that of *G. monostachya*, though considerably higher than that of *G. lingulata*. These facts are consistent with its preference for habitats intermediate between those preferred by the other two species.

Guzmania lingulata (L.) Mez

G. lingulata occurs mainly on sheltered ridges, and the majority of individuals is found on the lower branches and boles. It exhibits no marked trends with increasing altitude; while there are 93 individuals at 700 m and 80 individuals at 800 m, there are only 10 individuals at 750 m. It is almost absent from leeward slopes, and is rare on windward slopes; the population density in gullies is also low. These observations indicate a preference for moderately- to well-shaded habitats.

Pittendrigh (1948) states that *G. lingulata* is a shade-tolerant epiphyte, occurring in Trinidad in areas where the annual rainfall exceeds 1750 mm; he observed, nevertheless, that it occurs at maximum frequency in well-lit yet humid habitats, for instance, on branches overhanging rivers and streams, and where annual rainfall is between 3125 mm and 5000 mm. In Jamaica it is usually confined to more shaded situations or very humid mist forests (Laessle, 1961). Benzing & Renfrow, (1971a, 1971b) have shown that *G. lingulata* has a lower compensation point than *G. monostachya* and that its photosynthetic efficiency at low light intensities is higher. Also, it has a much lower percentage cover of trichomes than *G. monostachya* (Benzing & Burt, 1970) which is consistent with a preference for more humid habitats.

Guzmania sanguinea (André) André ex Mez

Like the previous species, *G. sanguinea* exhibits a preference for sheltered ridges, on which its population density varies from 26 individuals/plot at 650 m to 472 individuals/plot at 800 m; most of the increase with altitude takes place between 750 m and 800 m. It is notably rare in all other habitats, except the gully sampled in Plot 13, where 36 individuals were recorded. The populations above and below half canopy height are similar when the population density is high, as on the sheltered ridge at 800 m (Plot 7); where the density is lower, a higher proportion of the individuals occur on the lower branches and boles. Many indiviudals are terrestrial, usually on outcropping moss-covered boulders. Red pigmentation of the leaves becomes more prominent with increasing altitude.

TABLE 2. Numbers of each bromeliad species in 98 m^2 plots sampled in the four habitats discussed in the text. The top left figure is the number of individuals above 'half-canopy height,' and the bottom right figure is the number below 'half-canopy height.'

	windward		sheltered ridge					inter-mediate	leeward				gully	
Plot number Altitude	1 600	2 700	3 600	4 650	5 700	6 750	7 800	8 700	9 550	10 550	11 600	12 600	13 650	14 650
T. bulbosa												51 41		5
G. monostachya	2		30	4	40			2	44	68	80	98	6	1 35
T. anceps			47	1 53	2	3	3	15	2	2	14	15		1
G. lingulata	1 6		5 28	41	36 57	10	16 64	8 36			1	1	1 9	1 35
G. sanguinea	8		3 44	9 17	34 32	34 43	248 224	9 24			3	4	7 29	1 1
V. splendens						2 73	15 24	440 93						
V. heterandra	469 29	23 12	225 29	367 44	287 22	491 27	1131 21		70 8	185 9	197 19	86 24	147 19	147 36
G. cylindrica	28 91	19 177	8	1 1	25 14	30 40							9	1

In Trinidad, *G. sanguinea* is a light-demanding species that grows where annual rainfall exceeds 3125 mm, reaching maximum frequency in localities with an annual rainfall of ca. 5000 mm (Pittendrigh, 1948).

Vriesia splendens (Brogn.) Lem. var. **formosa** Suringer ex Witte

This species was encountered only on sheltered ridges above 700 m, and only 17 of the 114 individuals counted in Plots 6 and 7 were growing above half canopy height. This suggests a strong preference for sheltered, shaded sites. Pittendrigh's observations in Trinidad showed that *V. splendens* var. *formosa* (under the synonym of *V. longibracteata*) occurs in habitats where rainfall exceeds 2250 mm, and attains maximum frequency in the wettest zones, that is, where rainfall is more than 5000 mm. It has a higher humidity requirement than *G. lingulata* in Trinidad, and is commonly found in intense shade close to the ground. In Guyana, where it has been found from sea-level to 900 m (Smith, 1971), it has usually been recorded in moist habitats, often in forests below and around waterfalls where spray and fine mist give rise to continuous high humidity and fine precipitation.

Vriesia heterandra (André) L. B. Smith

Of the eight bromeliad species eoncountered in the cloud forest, *Vriesia heterandra* is the only one that occurs in every plot and in sizeable quantities in every habitat. Unlike the others, most of its individuals grow in the canopy; 90%of the total observed were above half-canopy height. There are distinct variations in population density both between and within habitats. On sheltered ridges the population is four times greater at 800 m than at 600 m; on windward slopes, this trend is reversed, and the numbers decrease with increasing altitude. These observations characterize *V. heterandra* as a light-demanding species with a tolerance of all but the strongest winds.

Some of the morphological features of *V. heterandra* which may be adaptations to the high solar radiation and concomitant drying effect in its preferred microhabitat are its small size, its dense rosette of narrow leaves and its tendency to form tight clumps of vegetatively reproduced individuals. It also impounds water in small quantities in the leaf axils, as well as having the morphological characteristics of an atmohpheric species. There is no information concerning its physiology. *Vriesia heterandra* has a wide ecological range, occurring in Andean habitats from 400-2300 m (Smith, 1977); the type specimen was collected in the Andes of Bogotá, at Puente de Quetame, where the annual rainfall is at least 2000 m (Wernstedt, 1972).

Guzmania cylindrica L. B. Smith

This is the only species which exhibits a strong preference for windward slopes (Plots 1 and 2). It also has sizeable populations on sheltered ridges at 650 m and 700 m, but is very rare or absent from other habitats. On windward slopes the plants are attached to the host tree below half-canopy height much more frequently than above, but since they are large and the canopy is very low, the rosette may extend into and even above the crowns. On the highest windswept slope of Cerro Huarech (852 m). *G. cylindrica* is effectively dominant over the woody vegetation, in terms of both height and numbers. Where it occurs in quantity on sheltered ridges, a higher proportion of individuals are anchored in the crotches of the larger upper branches.

There are no published data with which to compare these observations, since *G. cylindrica* is a rare species which has been collected from only two localities (Smith, 1977); the type specimen was collected in the Serranía de

Macuira by Romero Castañeda, and it has since been collected from Cerro Negro, Sierra de Aroa, Yaracuy, Venezuela, which lies some 350 km to the southeast. The observations reported here suggest a requirement for strong light, and therefore a restriction to windward slopes and the crotches of large branches because of its large size and weight, which probably prevent its establishment in the wind-disturbed canopy of taller trees. *Guzmania cylindrica* has several morphological attributes which are suitable for withstanding the effects of persistent high winds, in particular, its large size and sturdiness, well-developed anchoring, and its deep tanks which clearly guard against desiccation during cloud-free periods.

CONCLUDING REMARKS

These observations tend to confirm that precipitation through droplet interception by the vegetation increases with altitude, clearly as a result of the longer periods of cloud cover near the summits and the increased cloud flux brought about by the stronger winds. They also demonstrate that there are significant microclimatic differences between the various habitats, with windward slopes and sheltered ridges intercepting more moisture than leeward slopes or gullies. Progress up a leeward slope to a ridge is marked by sequence of bromeliad species, commencing with the dry-adapted heliophilic species *Guzmania monostachya* and occasional colonies of *Tillandsia bulbosa*; as the ridge is approached, the quantity of *G. monostachya* decreases significantly and the moisture-requiring species, *G. lingulata* and *G. sanguinea*, increase in number, reaching a peak of abundance at the ridge itself. The quantity of *Vriesia heterandra* in the canopy also increases, enchancing the deeper shade cast by the thicker tree crowns on the ridge. The higher precipitation on the ridge, it is suggested, is brought about by three factors. Firstly, though the forest floor is sheltered, the canopy projects into the airstream, following for several meters the slope of the adjacent windward slope (Figure 1); thus there is a greater cloud flux than on the leeward slope further down. Secondly, the canopy itself is much more dense than that of the leeward slope, and has a greater surface area for cloud interception. Thirdly, quite large drops of water were observed to blow over from the canopy of the vegetation on the adjacent exposed slope. A further factor which enhances the relative dryness of the leeward slope is increased insolation resulting from the more open canopy, which would have the effect of raising leaf temperatures and of hastening transpiration and the evaporation of surface moisture deposited at night by the clouds.

Gully habitats, like the sheltered ridges, have a fairly thick and shading canopy and consequently lower evapotranspiration rates in the understorey than leeward slopes. In general, however, they have a low cloud flux and, therefore, low precipitation levels. It may be suggested that the relative lack of atmospheric moisture precludes the development of large numbers of *Guzmania lingulata* and *G. sanguinea.* The population density of *Vriesia heterandra* is lower than on sheltered ridges, which also testifies to the discrepancy in cloud interception levels in the two habitats.

Windward slopes undoubtedly experience a greater throughput of cloud than any other habitat. The low stature of the vegetation may reduce the amount of moisture intercepted, but this must be more than compensated for by the very strong winds. In spite of this, the species requiring high moisture levels are rare, particularly at higher altitudes. This may be attributed to the drying effect of the wind during cloud-free periods, and the mechani-

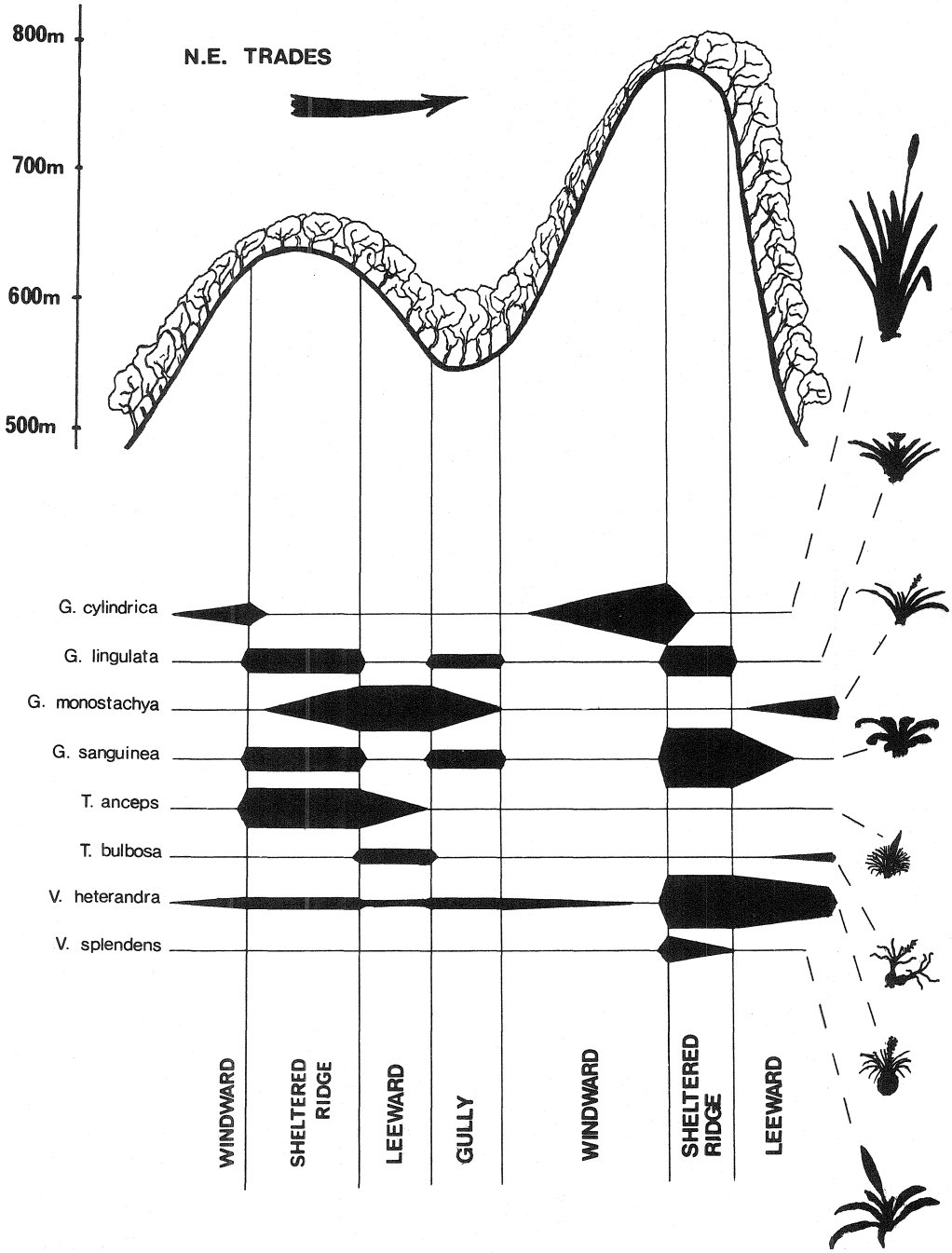

Figure 1. A qualitative summary of the results presented in Table 2, showing the distribution of bromeliad species in the various habitats of the cloud forest. Note how canopy height decreases with increased exposure to wind. The shaded bars indicate the commonness or rarity of each species in each habitat, rather than their frequency relative to other species. The silhouettes indicate the relative size of the bromeliad species (see Table 1).

cal difficulties encountered during establishment and growth. *Guzmania lingulata* and *Vriesia splendens* var. *formosa* have relatively flexible leaves which probably cannot withstand continual buffeting, while *Guzmania sanguinea*, in spite of having tougher leaves, would clearly be at a disadvantage on windward slopes due to its flattened, spreading rosette, which exposes a large surface area of leaves and tank-water to the winds. *Guzmania cylindrica* alone is capable of successful growth on the higher windward slopes, due to the morphological characters already discussed.

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